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Water relations of seedlings of Scots pine grown in peat as a function of soil water potential and soil temperature

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Abstract

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Seedlings of *Pinus sylvestris*, grown in low humified peat, were exposed to different soil water potentials (Ψ_s) and soil temperatures. The water potential and temperature were controlled by the use of a semi-permeable membrane system, and the seedlings were placed in a growth chamber during the experiments. Needle water potential (Ψ_s), needle conductance (g_n) and plant water conductance (G_p) were measured on the seedlings. When the soil water potential decreased to −0.1 MPa, the g_n decreased to about 25% of the maximum whereas the G_p decreased even more. The results are discussed in relation to resistance to water flow in the soil and in the root-soil interface.

Soil temperature in a interval of 5−25°C did not markedly change the relative response of g_n and G_p on Ψ_s. However, water uptake was considerably lower at lower soil teperatures, G_p at 7°C only being about 30% of that at 25°C soil temperature.

Water uptake was negatively affected by replanting in combination with drying the roots especially at low soil water potentials.

Key words: Pinus sylvestris, soil water potential, soil temperature, needle water potential, needle conductance, plant water conductance.

ODC 181.31:114.1:174.7 *Pinus sylvestris.*

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Introduction

The water uptake is often a critical factor for the establishment of tree seedlings (e.g. Kozlowski 1966, Lüpke 1973, 1979, Tranquillini 1973). In many studies the water uptake in newly planted seedlings is found to be less than 50% of that in established ones (e.g. Örlander, 1986).

The soil water potential is a major factor affecting the transpiration. Thus, Lopushinsky & Klock (1974), working with five different North-American conifers, found a decline in transpiration at water potentials lower than about −0.2 MPa. There was a considerable difference between species, and for example at −0.5 MPa the transpiration rates varied from 36 (*Pinus ponderosa*) to 63% (*Abies grandis*) of their maximum rates. Havranek & Benecke (1978) found that the transpiration in *Pinus cembra* decreased to about 50% of maximum rate at −0.3 MPa. Two studies concerning *Pinus sylvestris* (Rutter & Sands, 1958; Jarvis & Jarvis, 1963) showed that transpiration did not decline considerably until the soil water potential decreased to −0.1–0.2 MPa.

The soil temperature is also important for the water uptake. The viscosity of water and the root permeability change with soil temperature (Kramer & Kozlowski, 1979) which makes it difficult for seedlings to absorb water at low soil temperatures (cf. Cooper, 1973). Furthermore, soil temperature may change the effect of soil water potential on the water uptake.

In a previous study (Örlander, 1986) the water uptake by planted seedlings of *P. sylvestris* seemed to be unexpectedly negatively affected by low soil water potentials. Since that study was performed in the field, it was difficult to isolate the effect of soil moisture from other covariating environmental variables, and therefore the present experiments were performed in a growth chamber.

Soil water potential can be controlled by immersing the root system into solutions of varying concentration of polyethylene glycol (PEG). However, plants grown in such a solution may absorb some PEG which could affect growth and nutrient uptake (e.g. Jackson, 1962; Lawlor, 1970; Resnik, 1970; Emmert, 1974; Janes, 1974). Polyethylene glycol may, furthermore, have other negative or toxic effects on the roots. The problem can, however, be overcome by separating the soil and roots from the PEG-solution with a cellulose dialysis membrane (Zur, 1966; 1967). The membrane system is only impermeable to large molecules, and it is therefore possible to control the matric soil water potential. After an equilibration period the osmotic potential in the PEG-solution will balance the matric soil water potential.

The main objectives of the present study were to examine the effect of low soil water potentials on the water uptake of container-grown Scots pine seedlings and to study whether soil temperature and the condition of the plant material influences the effect of soil water potential on the water uptake.

Material and methods

Plant material

Seedlings of Scots pine (*Pinus sylvestris* L.) were grown in containers (Paperpot 408, Lännen-Tehtaat OY, Finland), filled with low humified peat, (Hasselfors super fine, Hasselfors, Sweden), in greenhouses (25/15°C day-night temperature) at the University of Agricultural Sciences in Umeå. The seedlings were hardened naturally outdoors during the summer and autumn. The seeds originated from a seed orchard outside Umeå (Östteg) with clones from plus trees selected in Sweden from 64°N–65°N, 100–400 m elevation. The seedlings were kept in cold-storage during the winter (−4°C). Before the start of the experiments the seedlings were allowed to thaw in room temperature for 2 days and thereafter planted in well-watered peat and placed in a growth chamber, where they were kept for 5 days. The soil temperature of the peat was approximately 25°C during day.

Initial value

On the last day of the acclimatization period, before the seeedlings were placed in membranes, measurements were made twice on all seedlings of needle conductance (g_n), needle water potential (Ψ_n) and plant water conductance (G_p). The mean of the two measurements was calculated and is called the initial value (cf. Table 1).

Climate

The experiments were performed in a growth chamber. The photoperiod was 16 hours, and the photon flux density was approximately 275 $\mu E \cdot m^{-2} \cdot s^{-1}$ during the day.

Table 1. *Mean ± standard error of needle conductance (g_n) needle water potential (Ψ_n) and plant water conductance (G_p) when starting the experiments (= initial value). The seedlings were immersed into different concentrations of polyethylene glycol (PEG) after the measurement. n=5*

PEG-centration (g/kg H_2O)	g_n ($cm \cdot s^{-1}$)	Ψ_n (−MPa)	G_p ($\mu g \cdot cm^{-2} \cdot s^{-1} \cdot MPa^{-1}$)
Expt 1			
100	0.314±0.038	0.77±0.05	4.00±0.58
50	0.215±0.030	0.72±0.03	2.77±0.41
30	0.202±0.011	0.82±0.05	2.40±0.14
0	0.284±0.023	0.80±0.06	3.46±0.34
Expt. 2			
100	0.291±0.039	0.67±0.03	3.66±0.58
50	0.238±0.020	0.61±0.07	3.27±0.33
30	0.287±0.016	0.62±0.04	3.84±0.23
0	0.280±0.023	0.62±0.02	3.78±0.26

The light was stepwise increased during a period of 30 minutes in the morning and correspondingly reduced in the evening. The seedlings were exposed to a constant vapour pressure deficit during the day. The relative humidity (RH) was kept at 50±5% during the day and 90±5% at night. The air temperature was kept constant at 20±1°C during most of the light period and at 10±1°C at night.

Semi-permeable system

The soil water potential was controlled by use of a semi-permeable system rather similar to that presented by Tingey & Stockwell (1977) (Fig. 1). The soil substrate of each seedling was enclosed in a water-rinsed dialysis tubing (Spectrapor I, cut-off 6–8000 m.w.). The tubes (length about 30 cm, diameter 3.2 cm) were tied in the middle with a knot. One half of the tube was used to enclose the soil substrate of the seedling and the other was brought up to the top of the container. Five sets of five seedlings were placed in vessels containing 3 l solution of water and PEG 20 M (molecular weight 15–20000), making a total of 25 seedlings in each experiment. The tubes were held upright with a holder made of narrow bands of stainless steel. The area of each pot exposed to the PEG-solution was 80 cm^2. The density of the peat was approximately 0.11 g dry weight/cm^3. The soil temperature was held at desired levels by controlling the temperature of the PEG-solution in the vessels. The roots were supplied with oxygen by bubbling air inside the membrane in the bottom of the pot.

The seedlings were immersed into four different concentrations of PEG 20 M: 0 g, 30 g, 50 g, and 100 g/kg H_2O. One vessel filled with 30 g PEG/kg H_2O was used as a control and was held at constant temperature (15°C) during the whole experiment. The controls showed reasonably constant water uptake during the experimental period and will therefore be omitted in the following. Preliminary studies revealed that constant soil water potentials were stabilized at desired levels after four days.

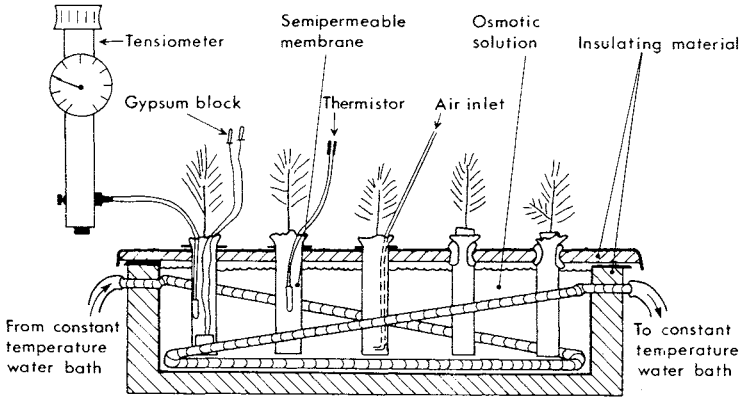

Fig. 1. Schematic diagram of the semi-permeable membrane system.

Experimental design

The water potential of the soil substrates was allowed to equilibrate with the PEG-solution at a soil temperature of ca 15°C. After the soil water potentials had equilibrated the soil temperature was changed and the water uptake was examined at three temperature levels.

Experiment 1

By regulating the temperature of the PEG-solution the soil temperature was kept at 15.7±0.3°C. After four days the soil temperature was lowered down to 6.8±0.3°C. Later the temperature was raised to 25.7±0.2°C and then decreased to 15.3±0.2°C. The equilibration time at each temperature was 24 hours.

Experiment 2

The roots of the seedlings were carefully washed out from the peat. They were then allowed to dry up in the laboratory (air temperature 23°C, RH 25%) for 30 minutes, before being replanted in the peat. After an equilibration time of 6 days with a soil temperature of 15.5±0.2°C, the soil temperature was changed to 25.1±0.1°C, then to 7.4±0.4°C and back to 15.8±0.2°C. The equilibration time at each temperature was 24 hours.

Soil water potential

Soil water potential (Ψ_s) was measured with tensiometers (Soil moisture eq., Santa Barbara, California, USA). The porous cup of a miniature tensiometer was placed in the middle of each pot, just inside the membrane. In the treatment with 100 g PEG/kg H_2O gypsum blocks ("Slim model" Soil moisture eq.) were placed in the bottom of each pot. Since gypsum blocks are sensitive to soil temperature differences, and the resistance of a block can be changed by more than 1% per degree C, the measured resistances at different temperatures were recalculated to corresponding soil moisture at room temperature (20°C).

Soil temperature

Soil temperature was measured with thermistors (M 843, Siemens München, Germany) inserted in small cylinders of brass. They were placed in the middle of the pot.

Needle conductance

Needle conductance (g_n) measurements were made with a null-balance porometer (Licor LI-1600, Licor Inc, Nebraska, USA) equipped with a cylindrical chamber. Measurements were made on the top of each shoot, and a projected needle area of about 15 cm^2 was enclosed in the chamber. The needle area was measured with a Licor area-meter (Licor 3000). The apical bud was removed to avoid growth of new needles and increasing needle area during the experiments.

Needle water potential

Needle water potential (Ψ_n) was measured on detached needles with a pressure chamber (Scholander et al., 1965; Waring & Cleary, 1967). The pressure chamber was especially designed for coniferous needles (Djos, Uppsala, Sweden). In the meantime, between sampling and measurement, the needles were stored in darkness in tubes with 100% RH. During the first days in each respective experiment the Ψ_n-measurements were excluded in order not to disturb the plant by removal of needles. Both Ψ_n and g_n were measured in the morning between 8 and 10 a.m., i.e. 5–7 hours after the light was switched on. Diurnal measurement was made on a sample of two seedlings per treatment.

Vapour concentration deficit

Vapour concentration deficit (VCD) was calculated from the data on air temperature and relative humidity, measured with an Assman psychrometer. Needle temperature was set equal to the air temperature since the difference normally is small (cf. Whitehead & Jarvis, 1981).

Plant water conductance

Plant water conductance (G_p) was calculated from the formula (Hellkvist et al., 1980; cf. Whitehead & Jarvis, 1981; Passioura, 1982):

$$G_p = \frac{q}{\Psi_s - \Psi_n}$$

where q is the water flux/needle are, estimated from the formula

$$q = g_n \cdot VCD$$

Statistical calculations

Mean values, standard deviation and standard error were calculated for the registered data. The significance of the effect of different soil temperatures on g_n and G_p was tested by t-test of the quotient between the value at actual temperature and that at 15°C. Regression curves were developed by the use of the least square method and logarithmic transformations. The equations were corrected for logarithmic bias.

Results

About four days after start of the experiment the soil moisture equilibrated at different levels depending on the concentration of the PEG-solutions (Fig. 2). The soil in the containers did not reach complete equilibrium during the experiments, especially not in Expt. 2. However, only a small decrease was found during the period when the soil temperature was changed, day 4–day 7 in Expt. 1, day 6–day 9 in Expt. 2.

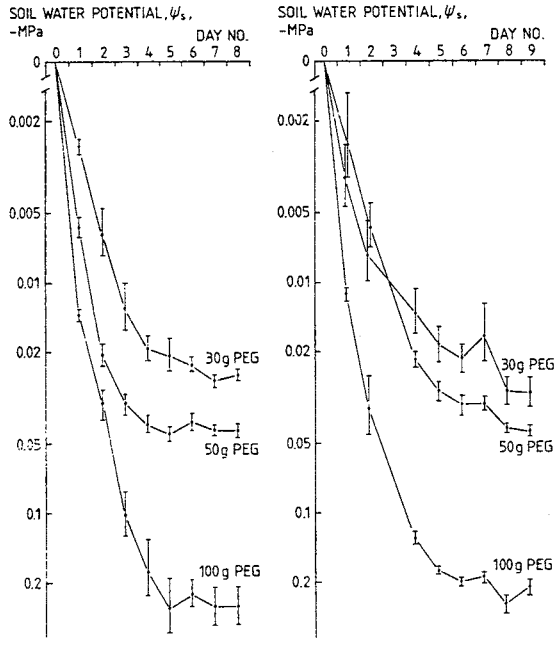

Fig. 2. Mean soil water potentials ± standard error (log scale) for seedlings of *Pinus sylvestris* immersed into different concentrations of polyethylene glycol (PEG). Expt. 1 (left) and Expt. 2 (right). $n=5$.

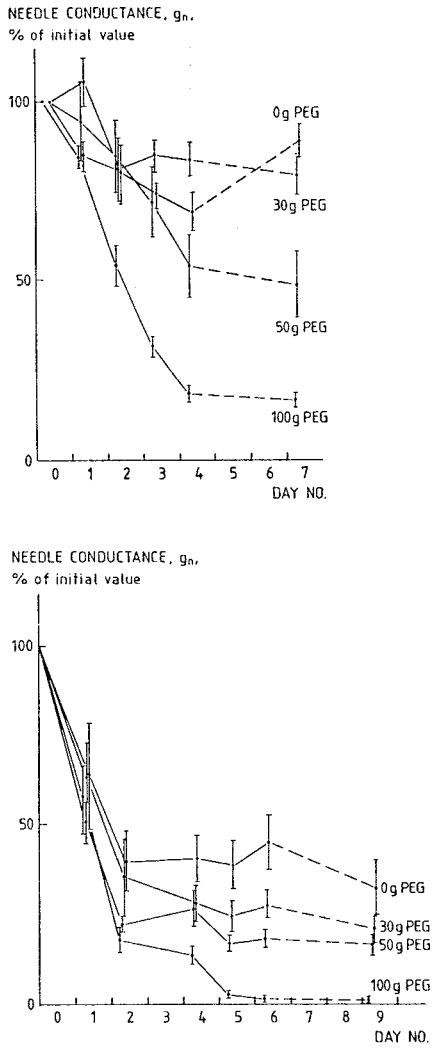

Fig. 3. Mean needle conductance (g_n) ± standard error for seedlings of *Pinus sylvestris* immersed into different concentrations of polyethylene glycol (PEG). Values are given in % of the initial values when watered (Table 1). The roots of the seedlings in Expt. 2 were first washed, then dried for 30 minutes and replanted. The dotted line refers to the days when the soil temperature was changed. Expt. 1 (top) and Expt. 2 (bottom).

The needle conductance declined in approximately the same way as did the soil moisture (Fig. 3). After four days in Expt. 1 and six days in Expt. 2, realtively constant g_n-values were found. The negative effect of drying up the roots and replanting the seedlings was evident (Fig. 3). Even in the well-watered pots the g_n in the root-dried and replanted seedlings was only 30–40% of the initial values. The effect of the different PEG-treatments was also evident, and the g_n of the seedlings in the most concentrated PEG-solution (100 g/kg H_2O) was ca 17% of the initial value in Expt.1 and only 2% in Expt.2. In Expt.1 the g_n in the seedlings immersed into water (Fig. 3) first decreased to about 70% (day 4), and later increased to about 90% (day 7) of the initial value. Since a probable reason for the decrease was insufficient oxygen supply during the first days, more air was bubbled into the soil during the latter part of the experiment, which probably explains the increase in g_n-values.

There was some daily variation in the g_n and Ψ_n (Fig.

4). The highest g_n values were found early in the morning, and the values decreased somewhat during the rest of the day. During the period of full light, constant temperture and relative humidity from 5 a.m. to 7 p.m. both g_n and Ψ_n were relatively constant.

The positive effect of increasing soil temperature and the negative effect of decreasing soil water potential on the water uptake was clear in both experiments (Fig. 5). The temperature effect was almost similar in relative terms at all levels of soil water potentials, and the g_n at 7°C was about 40% of the g_n at 25°C. The corresponding value for the G_p was about 30%.

Both g_n and G_p were negatively affected by a small decrease in soil water potential (Figs. 6, 7). The fitted regression lines of g_n and G_p versus soil water potential show that the water uptake had decreased considerably already at a water potential of −0.05 MPa. In Expt. 1 the g_n-value at a soil water potential of −0.1 MPa was ca 25%, and the G_p was ca 20% of that at −0.01 MPa (Figs. 6, 7). Corresponding values in Expt. 2 were about 14% (g_n) and 11% (G_p) (Figs. 6, 7, soil temperature 7°C excluded). The decrease in g_n and G_p in relative terms at low soil water potentials was thus larger in Expt. 2 than in Expt. 1.

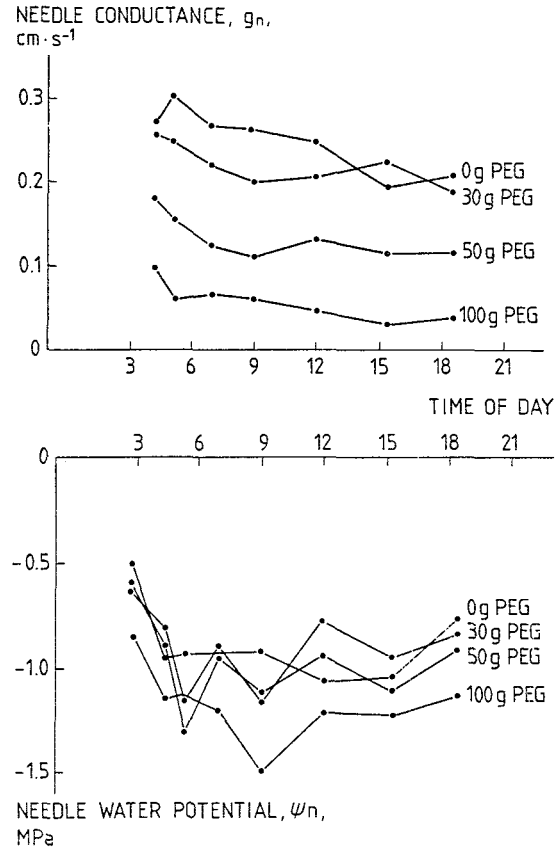

Fig. 4. Diurnal variation in needle conductance (g_n) and needle water potential (Ψ_n) during the last day of Expt. 1, for seedlings of *Pinus sylvestris* immersed into different concentrations of polyethylene glycol (PEG), $n=2$.

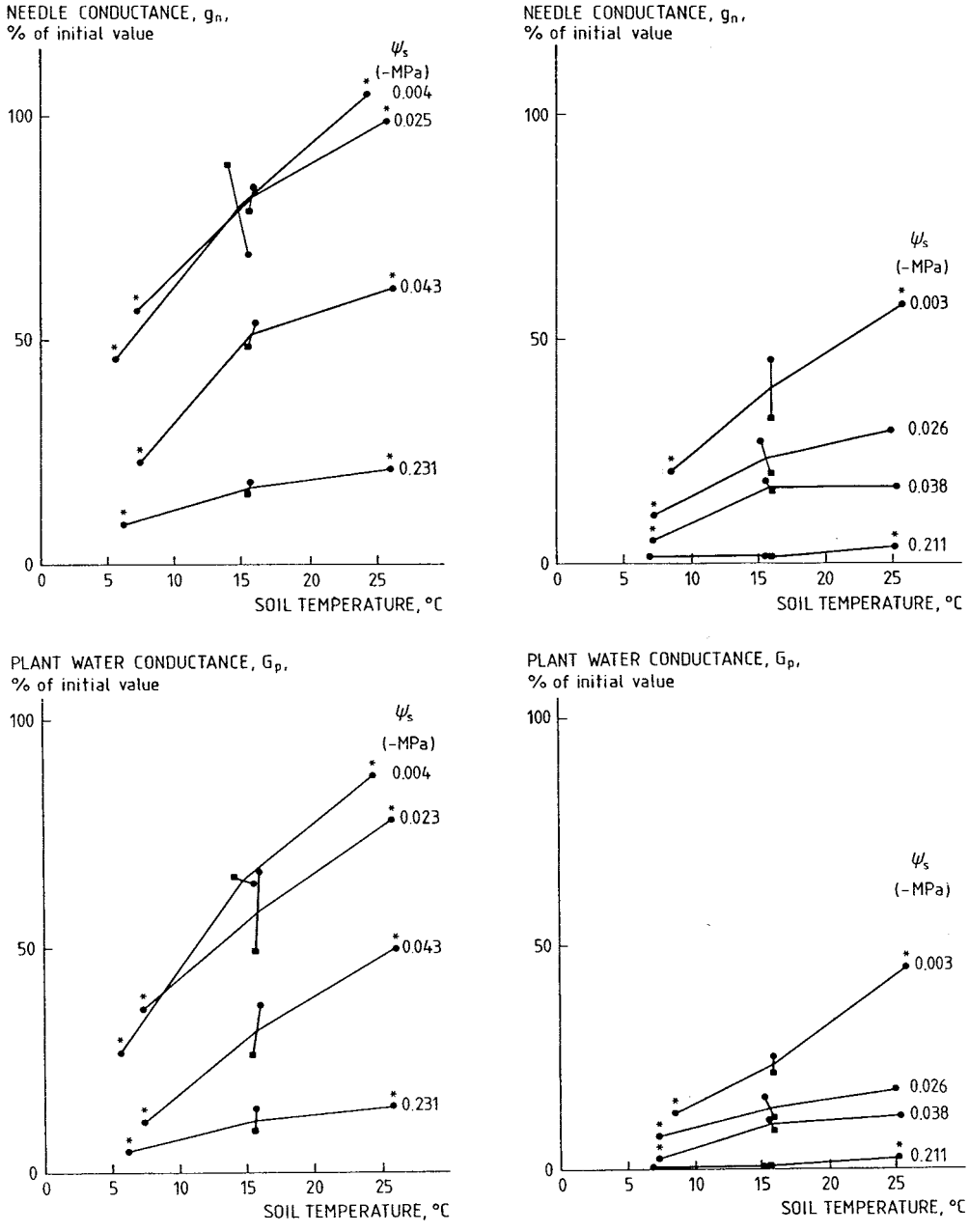

Fig. 5. Needle conductance (g_n) and plant water conductance (G_p) at different levels of soil water potentials (Ψ_s) and soil temperature. The value at a soil temperature of 15°C is the mean of the two measurements made before and after the change in temperature. ●=g_n or G_p before (■=after) the change in soil temperature. Expt. 1 (left) and Expt. 2 (right). Seedlings of *Pinus sylvestris*, n=5. ★=significant difference (p<0.05) from value at 15°C.

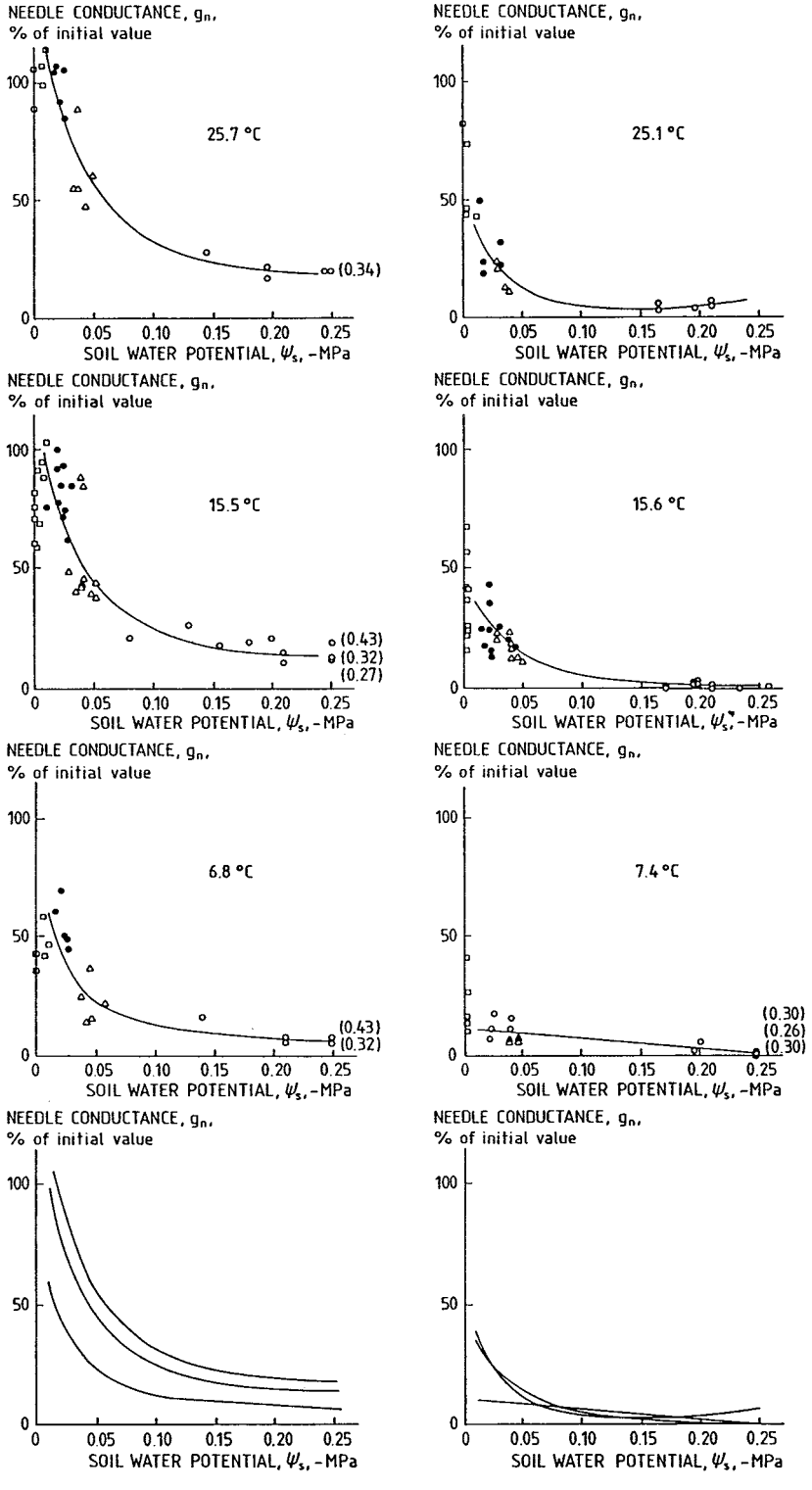

Fig. 6. The relation between needle conductance (g_n) and soil water potential (Ψ_s) at three levels of soil temperature. Regression curves are grouped for comparison at the bottom of the figure. Seedlings of *Pinus sylvestris* were immersed into different concentrations of polyethylene glucol (PEG). □=Og PEG/kg H_2O, ●= 30g PEG/H_2O, △=50 g PEG/kg H_2O, ○=100 g PEG/kg H_2O. Expt. 1 (left) and Expt. 2 (right). Values obtained at Og PEG/kg H_2O are not included in the regression line. Ψ_s values lower than −0.25 MPa within brackets.

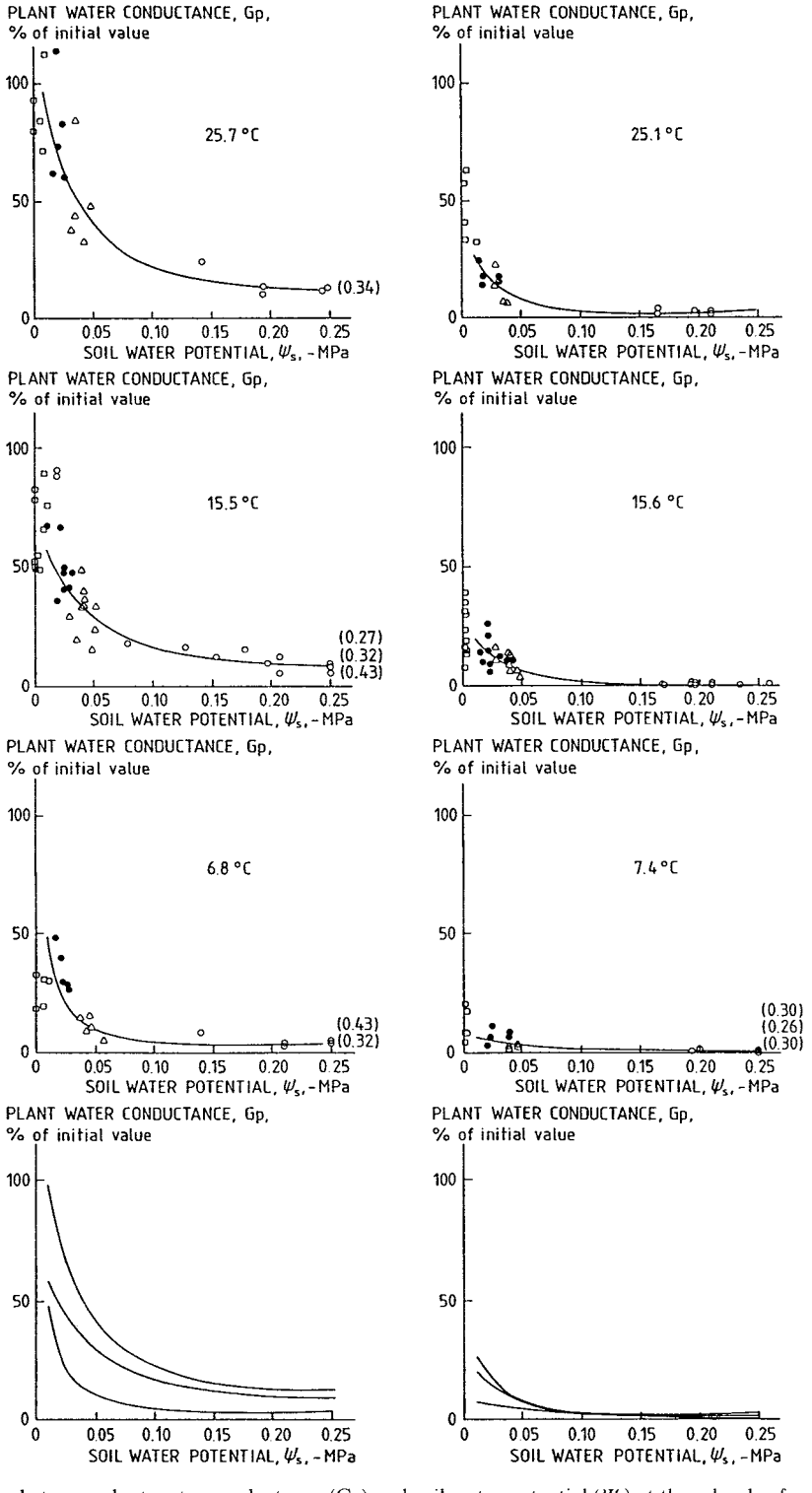

Fig. 7. The relation between plant water conductance (G_p) and soil water potential (Ψ_s) at three levels of soil temperature. Regression curves are grouped for comparison at the bottom of the figure. Seedlings of *Pinus sylvestris* were immersed into different concentrations of polyethylene glycol (PEG). □=Og PEG/kg H_2O, ●=30 g PEG/kg H_2O, △=50 g PEG/kg H_2O, ○=100 g PEG/kg H_2O. Expt. 1 (left) and Expt. 2 (right). Values obtained at Og PEG/kg H_2O are not included in the regression line. Ψ_s values lower than −0.25 MPa within brackets.

Discussion

The most important finding in the present study was that the seedlings were very negatively affected by decreasing soil water potentials (Figs. 6, 7). When the roots were exposed to air and replanted (Expt. 2), the water uptake was even more decreased by low soil water potentials. Compared to some previously reported experiments with pines (Rutter & Sands 1958, Jarvis & Jarvis 1963, Babalola et al. 1968, Lopushinsky & Klock 1974, Havranek & Benecke 1978) the negative effect on water uptake because of low soil moisture was very pronounced. When expressed as percentages of their maximum rates at a soil water potential of −0.1 MPa the transpiration in the various studies was: Lopushinsky & Klock (1974), 98% (*Pinus contorta*); Havranek & Benecke (1978), 72% (*P. cembra*); Babalola et al. (1968), 65% (*Pinus radiata*); Rutter & Sands (1958), 58% (*P. sylvestris*); Jarvis & Jarvis (1963), 46% (*P. sylvestris*). The above values were derived from each respective investigation. Corresponding values of transpiration in the present investigation were 14–25% of the maximum. The rooting medium varied considerably between the studies showing that the seedlings grown in more fine-textured substrates (clay, silt mixtures) were less negatively affected by low soil water potentials. In a planting experiment in sandy soil presented by Lüpke (1979) the transpiration in seedlings of *Pseudotsuga menziesii* decreased to about 35% when soil water potential was lowered from ca −0.01 MPa to ca −0.025 MPa. Obviously the plant material and the type of soil used in the experiments influence water uptake significantly at different soil water potentials.

A question which has been discussed for several years is why the total hydraulic resistance in the soil-plant-system increases when the soil dries (e.g. Molz, 1981). The theoretical analysis of water flow in the soil to the roots (e.g. Newman, 1974) predicts that the resistance in the soil surrounding the roots should be small and negligible. In several studies this theory is questioned and it is assumed that a considerable resistance could occur in the soil surrounding the roots or in the root-soil interface (*e.g.* Faiz T Weatherly, 1977; 1978; Herkelrath et al., 1977; Weatherly, 1982). The low water uptake found in the present study might therefore be explained either by a high resistance barrier from the root epidermis to the root xylem, or by high resistance to water flow in the soil surrounding the roots.

The largest drop in water potential within the plant is usually found in the root, from the root surface to the xylem (e.g. Passioura, 1982). The resistance from the root xylem to the needle is usually small and can be disregarded (e.g. Passioura, 1982). Different responses to decreasing soil water potential could therefore be explained by different conductivity within the roots. However, this assumes that the root conductivity changes rapidly with decreasing soil water potentials. No conclusive evidence in support of this hypothesis has been found. Furthermore, there is no explanation why the soil texture should influence the root conductivity. It might be more likely that the resistance in the soil surrounding the roots dominates the root resistance at low soil water potentials, at least in coarsely textured soils. Low humified peat has a lot of water bound in the peat fibres, and therefore hardly any water is present in the pores between the fibres in dry peat (cf. Päivänen, 1973). The unsaturated conductivity of low humified peat is consequently low, about the same as in coarse sand (Bartels & Kuntze, 1973): For example, the conductivity of a low humified peat decreased from 1.2 mm/day to 0.002 mm/day when the soil water potential decreased from −0.01 MPa to −0.1 MPa (Bartels & Kuntze, 1973). The drastic decrease in transpiration found by Lüpke (1979) when decreasing the soil water potential down to −0.025 MPa can be explained by a rapid decrease in conductivity in the sand.

The theories put forward by Herkelrath et al. (1977) provide an additional explanation why the water uptake decreases with decreasing soil water potentials. According to them an improtant resistance could occur at the root surface = the root-soil contact resistance. This resistance should be proportional to the volume saturation of the pore space or to the wetted fraction of the root surface. Soils with a large proportion of large pores, *e.g.* sand and low humified peat, could accordingly give high contact resistance when dry. Low water uptake in seedlings grown in soils of coarser texture has consequently been explained as a difference in contact resistance (Dosskey & Ballard, 1980). Additional contact resistance could occur because of root shrinkage (Huck et al., 1970) or by soil shrinkage. Planting of bare-root seedlings could also result in considerable contact resistance because vapour gaps are likely to be formed around the roots when planting.

In experiments with *Pinus strobus* and *Pinus resinosa,* Kramer (1942) found that transpiration at a soil temperature of 5°C was only about 50% of that at 25°C. The negative effect of low soil temperatures was even more pronounced in the present study (Fig. 5). However, in most experiments previously reported the water uptake suddenly decreases at a critical low soil temperature. An increase in soil temperature above that critical temperature should not increase the water uptake, as

reviewed by Whithead & Jarvis (1981). A soil temperature of about 3°C has been found to be critical for *P. sylvestris* seedlings (Linder, 1973). The discrepancy in effect of low soil temperature found in the present study and that of Linder (1972) could be that the seedlings have to be exposed to low soil temperature for a longer time than that used by Linder before the full effect of the temperature change can be detected. In the present study it was found that at least one day was needed before the g_n and G_p stabilized after a change in temperature. Differences in the plant material could also have caused the difference in result, since Linder worked with hardened seedlings (cf. Christersson, 1972) which were considerably larger and consequently had larger storages of water, than those used in the present study. The soil temperature may, finally, be important for the hydraulic resistance in the soil outside the root as, for example, the viscosity of water is temperature dependent. This might also have influenced the result.

There was no tendency in the present experiments that the relative effect on g_n and G_p of lowering the soil water potentials should differ depending on the soil temperature (Figs. 6, 7, Expt. 2, soil temperature 7°C excluded). The shapes of the regression lines were approximately the same independent of temperature, although on different levels.

The effect of drying the roots and replanting the seedlings was that the water uptake decreased especially at low soil water potentials. The effect could either be due to a lower seedling quality or simply to the fact that the seedlings were replanted.

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